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Ethology of Three Southern African Ground Nesting Masarinae, Two *Celonites* Species and a Silk-spinning *Quartinia* Species, with a Discussion of Nesting by the Subfamily as a Whole (Hymenoptera: Vespidae)

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Abstract.— Accounts are given of some aspects of the nesting of *Celonites latitarsis* Gess, *C. wahlenbergiae* Gess and *Quartinia vagepunctata* Schulthess. *Celonites latitarsis* nests in sandy soil, excavating a sloping burrow terminating in a cell in which it constructs an earthen cell. *C. wahlenbergiae* uses a pre-existing burrow in which it constructs linearly arranged earthen cells. Both species collect soil for cell construction from a quarry at some distance from the nest and circumstantial evidence suggests that both use nectar as the bonding agent. *Quartinia vagepunctata* excavates a vertical burrow surmounted by a turret and terminating in a cell, the whole being stabilized by the use of self generated silk as the bonding agent. In order that the nesting accounts should be put into context, nesting by the Masarinae (*sensu* Carpenter 1982) as a whole is outlined and discussed.

Celonites Latreille and *Quartinia* Ed. André are two Old World masarine genera. *Celonites* occurs in the Palaearctic Region in the countries bordering the Mediterranean Sea, northwards to Switzerland and southern Germany and eastwards to Transcaspia and southwestern Iran, and in the Afrotropical Region in north east Africa and southern Africa (Richards 1962). In southern Africa the genus has a southern and western distribution with the greatest number of species having been recorded from the western areas (Richards 1962, Gess and Gess 1989, label data Albany Museum).

Around thirty species of *Celonites* are known, nearly half from southern Africa. Little has been recorded concerning their nesting behaviour due undoubtedly to the cryptic nature of the nests. Brief notes have been published on the nests, all aerial, of six species as listed in the discussion. It seemed likely that *Celonites* as a genus would be found to construct aerial nests. The present accounts of ground nesting by *C. latitarsis* Gess and *C. wahlenbergiae* Gess therefore, although based on only one nest each, add considerably to the knowledge of the nesting behaviour of the genus.

Quartinia occurs in the Palaearctic Region bordering the Mediterranean Sea and extends eastwards into Asiatic Russia and India, and in the Afrotropical Region in southern Africa (Richards 1962). In southern Africa the genus has a largely southern and western distribution with, like *Celonites* the greatest number of species having been recorded from the western areas (Richards 1962, Gess and Gess 1989, label data Albany Museum).

Around fifty species of *Quartinia* are known, more than half from southern Africa. Concerning the nesting behaviour of this genus there seems to be only one casual observation listed in the discussion. The present account for *Q. vagepunctata* Schulthess, which uses silk for stabilizing its turret, burrow and cell walls is therefore of particular interest.

The investigations presented in the present paper were undertaken during the course of two field trips to the southwestern Cape in early summer, September/October, of 1989 and 1990.

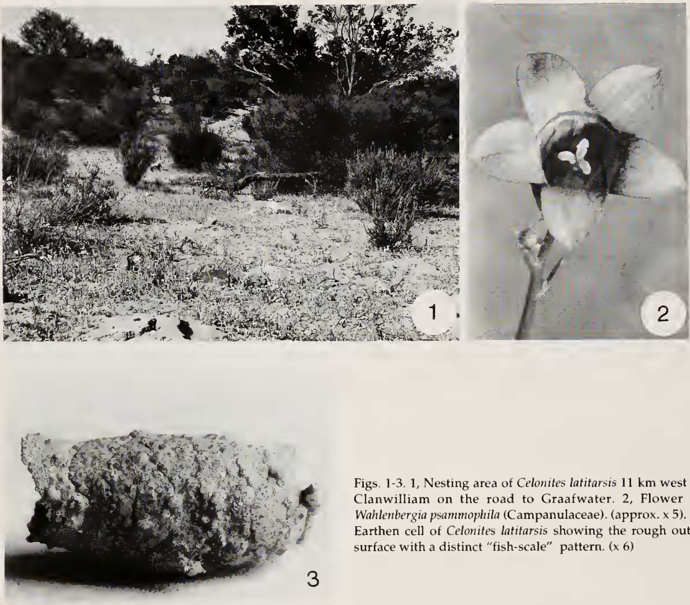
Voucher specimens from these studies are deposited in the Albany Museum.

ETHOLOGICAL ACCOUNTS

Celonites latitarsis Gess

Geographic distribution and description of nesting area.— *Celonites latitarsis* has as yet only been recorded from the type locality, 11 km west of Clanwilliam on the road to Graafwater (Fig. 1) in

[1]The order of names is alphabetical and equal joint authorship should be understood.



Figs. 1-3. 1, Nesting area of *Celonites latitarsis* 11 km west of Clanwilliam on the road to Graafwater. 2, Flower of *Wahlenbergia psammophila* (Campanulaceae). (approx. x 5). 3, Earthen cell of *Celonites latitarsis* showing the rough outer surface with a distinct "fish-scale" pattern. (x 6)

the hilly area between the Olifant's River Valley and the sandy coastal plain.

The vegetation is characterized by the presence of Restionaceae, shrubby Proteaceae and scattered *Aspalathus spinescens* Thunb. (Fabaceae) with a sparse general ground cover of predominantly *Wahlenbergia psammophila* Schltr. (Campanulaceae) and *Helichrysum* cf. *hebelepis* DC. (Asteraceae), and a moist ground cover of *Monopsis debilis* (L.f.) Presl.(Lobeliaceae). It is best categorized as "Dry Mountain Fynbos", as described by Moll et al. (1984), with an intrusion of sandveld elements on disturbed ground.

The soil is sandy, relatively coarse and loose on the surface but finer and more compact beneath. The finer sand is brought to the surface by the Cape Dune Molerat, *Bathyergus suillus* (Schreber) (Bathyergidae) which is common in the area. The molehills stabilize forming "hillocks" of compacted sand suitable for the excavation of burrows and used for this purpose by *Scrapter* (Colletidae), *Belomicrus* and *Bembecinus* (both Sphecidae). The nest of *C. latitarsis* was sited in the gently sloping side of such a "hillock" which was almost entirely covered with loose sand and was sited at the base of a small, dry, dead shrub.

Plant visiting.— All plants in flower were sampled for flower visitors. Females and males of *C. latitarsis* were visiting flowers of *Wahlenbergia psammophila* (Fig. 2) in company with *Celonites wahlenbergiae* Gess, *Celonites bergenwahliae* Gess and *Masarina mixta* Richards (also Masarinae). Apart from *W. psammophila* the only plant species from which *C. latitarsis* was recorded was *Coelanthum grandiflorum* E. Mey ex Fenzl (Aizoaceae) (1 male).

On sunny days activity on *W. psammophila* flowers was from mid morning, when the flowers opened, until late afternoon, when the flowers closed. The exact times of flower opening and closing and masarine activity varied according to the weather.

Females of *C. latitarsis* visiting *W. psammophila* flowers entered up to eight flowers in succession, usually on different plants. They always alighted on the outwardly curved free tip of a corolla lobe before entering the flower.

Provision.— Pollen from the provision taken from the nest and examined microscopically was all of one type and matched that of *W. psammophila.*

Description of nest.— Only one nest of *C. latitarsis* was located. It consisted of an arched entrance leading to a short sloping burrow of diameter 4,5 mm terminating at a depth of 35 mm in a horizontal excavated cell of diameter 5 mm. Within the excavated cell was a constructed earthen cell of the same diameter as the excavated cell (Figs 3 and 4).

The earthen cell is roughly ovoid with a slightly flared lip extending beyond the neck. It is 10 - 11 mm in length, the lip being uneven. The outer diameter at the widest point is 5 mm and at the neck 4 mm. The cell walls are extremely hard, the sand grains being very firmly cemented together. The outer surface is rough and has a visible "fish scale" pattern. The inner surface is smoothed. The cell is still open, provisioning not having been completed.

Method of construction of the nest, oviposition and provisioning.— There are two distinct phases in nest construction; burrow excavation and cell construction. Sand removed during burrow excavation is not used for cell construction. Sand for this purpose is mined at some distance and carried into the burrow. The burrow entrance is left open while the wasp is away from the nest.

At 11h00 on 3.x.1990 a female *C. latitarsis* was seen to be initiating a burrow. Sand excavated from the burrow was drawn out by the wasp as she reversed out of the burrow to a distance of approximately 20 mm down slope from the burrow entrance, where it accumulated forming a tumulus. From time to time a certain amount of raking of the "path" to the burrow took place. Also from time to time the wasp flew up, circled and returned.

At 11h52 burrow excavation had been completed and cell construction commenced. During cell construction the wasp made regular visits to a quarry site on a stabilized molerat "hillock" approximately 2,5 m from the nest. When at the quarry site, the wasp vibrated up and down vigorously whilst scraping up a load of sand. The visits to the quarry, each taking an average of 29

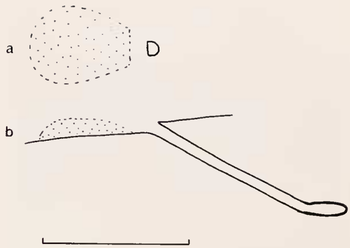


Fig. 4. Diagrams of nest of *Celonites latitarsis*: a. nest entrance and tumulus from above; b. vertical plan. (Scale bar = 50 mm).

seconds (n = 36), alternated regularly with periods in the nest. Each period in the nest during which the building material must have been added to the cell lasted an average of 48 seconds (n = 37). After five to seven successive visits to the quarry the wasp visited a succession of *W. psammophila* flowers and was then lost to sight for 10-20 minutes. On her return she alighted at either the nest or the quarry site. It is presumed that she was collecting liquid to mix with the dry sand to make it malleable for cell construction. As the cell walls are harder and more durable than they would be had water been used and as *C. latitarsis* has never been observed at water it seems probable that the liquid collected was *W. psammophila* nectar.

At 14h00 after approximately 36 additions to the cell, the wasp flew off to visit a succession of *W. psammophila* flowers. After an absence of 49 minutes she reappeared. Instead of going to the quarry she returned directly to the nest. After a period of 11 minutes 45 seconds in the nest, during which it is probable that oviposition took place, she flew off to the flowers. Provisioning had commenced. A regular pattern of flower visiting alternating with a period in the nest continued until 16h00 when the wasp entered the nest and did not reappear.

At 17h00 it was decided that the wasp's work for the day was over. The nest was then investigated and the female which was sheltering in the cell was collected.

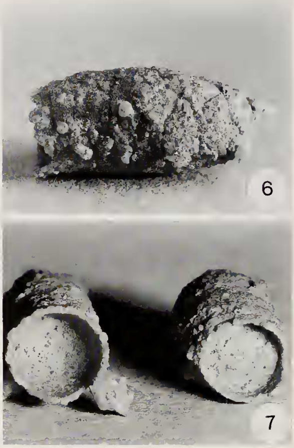
Male behaviour.— No males were seen in the vicinity of the nest.

Celonites wahlenbergiae Gess

Geographic distribution and description of nesting area.— *Celonites wahlenbergiae* Gess has been recorded from three sites in the Clanwilliam District, one at the Clanwilliam Dam and two on the road to Graafwater at 5 km and 11 km west of Clanwilliam. At all sites it has been associated with *Wahlenbergia*. Despite intensive collecting on *Wahlenbergia* in areas beyond the Clanwilliam District it has not been found, suggesting a relatively restricted distribution.

A nesting area of *Celonites wahlenbergiae* was located on the eastern side of the Clanwilliam Dam on a sparsely vegetated slope above the caravan park. The vegetation in the immediate vicinity of Clanwilliam is classified as a "Mosaic of Dry Mountain Fynbos and Karroid Shrublands" (Moll et al. 1984). That of the nesting area of *C. wahlenbergiae* is best described as depauperate dry fynbos. The dominant shrub is *Aspalathus spinescens* Thunb. (Fabaceae). Ground cover is sparse. The dominant low growing plant is *Wahlenbergia paniculata* (Thunb.) A.DC. (Campanulaceae). The soil is of the same nature as that at the *C. latitarsis* nesting site and is similarly subject to mole rat activity.

Plant visiting.— *Celonites wahlenbergiae* has been found commonly associated with deep flowered *Wahlenbergia* species: with *W. paniculata* (as *W.* sp. A in Gess 1989, Gess and Gess 1989) at Clanwilliam Dam; with *Wahlenbergia costata* A.DC. 5 km west of Clanwilliam; and with *Wahlenbergia psammophila* 11 km west of Clanwilliam. In all cases where the wasp was found *Wahlenbergia* was in flower in abundance. It is of interest that the large, shallow flowered, *Wahlenbergia annularis* A.DC., which was flowering abundantly in the areas where *C. wahlenbergiae* was present, was never visited by these wasps although it was visited for nectar and pollen by melittid bees.



Figs. 6, 7. 6, Earthen cell of *Celonites wahlenbergiae* showing the rough outer surface with a distinct "fish-scale" pattern. (x 6). 7, End on views of the earthen cells of *Celonites wahlenbergiae*. On the left is shown the smoothed inner surface of an incomplete cell; on the right is shown the seal of a completed cell. (x 6).

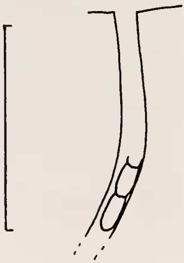


Fig. 5. Vertical plan of nest of *Celonites wahlenbergiae*. (Scale bar = 50 mm).

Celonites wahlenbergiae, however, is not restricted to *Wahlenbergia* species as it was visiting, in addition but less commonly, *Crassula dichotoma* L. (*Crassula*ceae) at Clanwilliam Dam; and *Coelanthum grandiflorum* E. Mey ex Fenzl (Aizoaceae), Herrea sp. (Mesembryanthemaceae), *Polycarena* sp. (Scrophulariaceae), *Helichrysum* cf. *hebelepis* DC. (Asteraceae), an unidentified composite and *Pelargonium* sp. (Geraniaceae) 11 km west of Clanwilliam. It, however, was not represented in samples of insects from other plants in flower, notably *Aspalathus spinescens* which is commonly visited by the masarines *Ceramius clypeatus* Richards and *Masarina familiaris* Richards.

Provision .— Provision from a fully provisioned cell was olive green, very moist and did not adhere to nor wet the cell walls. The pollen, examined microscopically, was found to be of two types, one matching only that from *Wahlenbergia paniculata* and the other only that from a *Coelanthum* species which was growing mixed with it.

Description of the nest.— The single nest of *C. wahlenbergiae* located consisted of three linearly arranged earthen cells attached to the wall of an apparently pre-existing burrow excavated in sandy soil. The burrow, of diameter 5,5 mm, descended vertically to a depth of approximately 30 mm after which it continued in a steep slope. Three cells, two sealed and the third in an early stage of construction, were positioned at the upper end of the slope (Fig. 5).

The completed cells are rounded at the inner end, roughly ovoid but with the sealed outer end truncate. They are 9 and 8 mm in length, and 4,5 and 4 mm respectively in outer diameter at the widest point. The outer diameter at the neck of each cell is 4 mm. The cell walls are extremely hard, the sand grains being very firmly cemented together. The outer surface of the cell wall is rough and shows a distinct "fish-scale" pattern (Fig. 6). The seal, constructed from the same material as the cell walls, is positioned within the neck of the cell (Fig. 7). The base of a succeeding cell is attached to the seal of a preceding cell so that it is positioned within the opening of that cell. The inner surface of the cells is smooth (Fig. 7).

Method of construction of the nest.— Nest initiation was not observed. A pre-existing burrow was probably used as the cells in the nest investigated were positioned on the burrow wall well above the inner end of the burrow and as their diameters were less than was that of the shaft.

Sand for construction of the cells was being quarried from the surface of a stabilized molerat "hillock" situated 3 m from the burrow. At midday on 19.x.1989 the wasp was seen visiting a *Crassula dichotoma* flower after which she flew to the quarry. At the quarry site she vibrated vigorously apparently loosening sand with her mandibles. Having gathered a load she flew with it to the burrow. Sand gathering was repeated several times. The wasp was then captured and the nest investigated.

As the cell walls are harder and more durable than would be expected had water been the bonding agent it is probable that nectar was used. *Celonites wahlenbergiae* has, notably, never been seen at water. It seems likely that the visit to *Crassula dichotoma* was for the purpose of collecting nectar.

Male behaviour.— No males were seen in the vicinity of the nest.

Quartinia vagepunctata Schulthess

Geographic distribution and description of nesting area.— *Quartinia vagepunctata* Schulthess has been recorded from 38 km west of Ceres, Calvinia, and Doorn River Falls (Richards 1962). It is here recorded from two sites on the western fringe of the Great Karoo (above the Nieuwoudtville Waterfall [= Richards' Doorn River Falls] and the Skuinshoogte Pass, 15 km north of Nieuwoudtville) and from six sites in Namaqualand (Goegab Nature Reserve to the east of Springbok; Narap, Klipfontein and the Wildeperdehoek Pass, all to the south west of Springbok; and Anenous to the north west of Springbok).

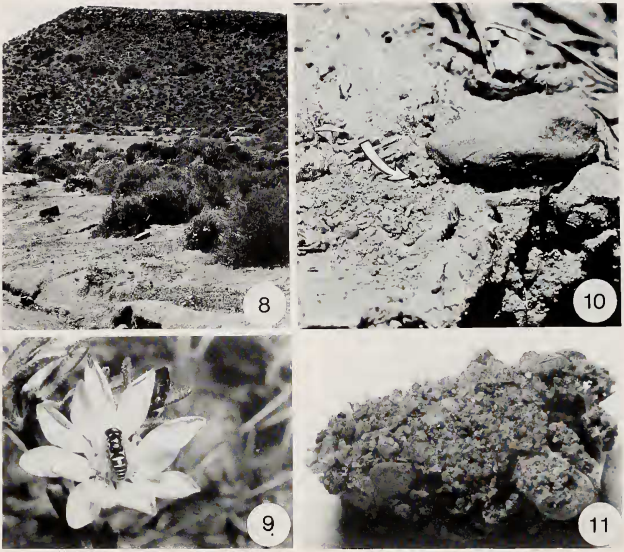
A nesting area of *Q. vagepunctata* was located in the Skuinshoogte Pass (Fig. 8). The vegetation is probably closest to Acocks' Veld Type 28, Western Mountain Karoo (Acocks 1953, 1975). The nesting site was a bare patch of somewhat uneven level ground between shrubs. The soil was sandy and friable.

The site approximately one square metre, was located in October 1989 and revisited in September 1990 when it was again being actively used for nesting.

Plant visiting.— *Quartinia vagepunctata* was foraging almost exclusively on Asteraceae: extremely commonly on flowers of *Relhania pumila* Thunberg (Fig. 9) in the Skuinshoogte Pass and *Leysera gnaphalodes* (L.) L. in the Goegab Nature Reserve, and at Narap and Anenous; and less commonly on flowers of *Leysera gnaphalodes* above the Nieuwoudtville Waterfall, *Cotula* cf. *leptalea* DC., *Senecio* prob. *niveus* Less., *Pentzia suffruticosa* (L.) Hutch. ex Merxm. and *Osteospermum* cf. *oppositifolia* in the Skuinshoogte Pass, *Pentzia suffruticosa* in the Wildeperdehoek Pass, ?*Helichrysum* sp. and *Cotula* sp. at Anenous.

The exceptions were a female collected on a low growing *Galenia* sp.(Aizoaceae) growing amongst *Leysera gnaphalodes* at Anenous and a male collected on a flower of *Lebeckia* cf. *sericea* Thunb. (Fabaceae) at Klipfontein. It is of interest that these were visiting flowers of families favoured by other masarines.

The flowers of all but two of these species were yellow. *Senecio* prob. *niveus* has whitish flowers and the *Galenia* sp. pink flowers.



Figs. 8-11. 8, Nesting area of *Quartinia vagepunctata*, Skuinshoogte Pass, 15 km north of Nieuwoudtville on the road to Loeriesfontein. 9, *Quartinia vagepunctata* on flower of *Relhania pumila* (Asteraceae). (approx. x 3). 10, Nesting site of *Quartinia vagepunctata*, arrow indicating sand and silk nest entrance turret. (approx. x 1). 11, Dorsal view of sand and silk nest entrance turret of *Quartinia vagepunctata*. (x 14,4).

Provision.— Provision from four nests of *Quartinia vagepunctata* investigated in the Skuinshoogte Pass was in the form of a relatively moist bright yellow nectar and pollen mass almost entirely filling the cell, adhering to the cell walls and therefore not forming a discrete pollen loaf. The pollen was examined microscopically. That from one nest was of one type only and matched that of *Cotula* and that from the other three nests was of two types mixed and matched that of *Relhania* and *Cotula*.

Description of the nest.— Seven nests of *Q. vagepunctata* were investigated, four on 7.x.1989 and three on 27.ix.1990. Each had its entrance to one side of an earth clod or stone (Fig. 10).

The nest consists of a subterranean silk-lined burrow surmounted by a horizontal turret (Figs 11 and 12), the outer surface of which is of sand (grain size: 0.16 mm - 1,2 mm) held together by a silk lining. The turret is bag-like, approximately circular in cross-section with its diameter greatest at its outer end and smallest at its inner end. The opening to the burrow entrance is at some little distance from the closed inner end of the bag.

The burrow in the nests investigated consisted of a subvertical shaft, 1,5-2 mm in diameter, terminating in a sealed roughly ovoid cell at depths of 25-30 mm. The cell walls were constructed of sand bonded together with silk and well cemented with an unidentified substance somewhat resinous in appearance. In one of the nests the female was found sheltering in a lateral shaft, suggesting that more than one cell per nest is probably constructed.

Method of construction of the nest.— The soil in which the nest is excavated is friable. Water is not required for nest excavation and is not used as a

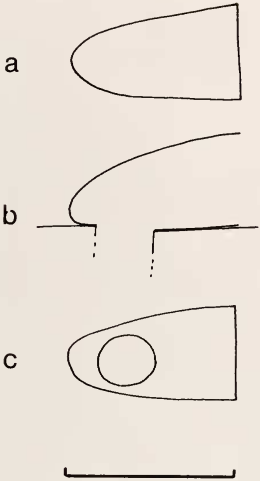


Fig. 12. Plans of turret of *Quartinia vagepunctata*. a. from above; b. vertical section; c. from below. (Scale bar = 5 mm).

bonding agent. It is therefore not surprising that *Q. vagepunctata*, though collected commonly at flowers, has never been collected at water.

The silk used in nest construction is spun by the nest builder. One individual was observed whilst it was joining together sand grains with silk. It was rotating its head and the silk was apparently issuing from its mouth suggesting that the silk may be produced by mandibular glands.

Male behaviour .— Males, unlike the females, were common on the ground in the vicinity of the forage plants. They were observed to rise up and mount females visiting these plants.

Males were also present at the nesting site.

Associated insects .— Several individuals of *Allocoelia moscaryi* (Brauns) (Chrysididae) were present in close proximity to the nests. As this chrysidid has in addition been found by the authors in association with three *Quartinioides* species and as all known *Allocoelia* associations are with masarines (Kimsey and Bohart 1990) it is suggested that this wasp is most probably a nest parasite of *Quartinia* and *Quartinioides*.

DISCUSSION

Richards (1962) saw the family Masaridae as constituted of three sub-families, the Euparagiinae, Gayellinae and Masarinae, and to be a "sister group" of the families Eumenidae and Vespidae in a superfamily the Vespoidea. Carpenter (1982) assessed the phylogenetic relationships of the components of the Vespoidea (*sensu* Richards) using cladistic methods. He treated Richards' Vespoidea as a single family Vespidae in which he recognized six subfamilies, Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Polistinae and Vespinae. He thereby disassociated the Euparagiinae which provision with beetle larvae from Richards' Gayellinae and Masarinae which provision with pollen and nectar. At the same time he associated more closely the Gayellinae (*sensu* Giordani Soika 1974) and Masarinae (*sensu* Richards 1962) by placing them together as tribes (Gayellini and Masarini) in his subfamily Masarinae. Following this grouping the present authors have excluded the Euparagiinae from their discussion. *Ceramius*, the most studied genus, is divided into species groups following Richards (1962) amended by Gess and Gess (1986, 1990).

In order that the nesting accounts for *Celonites latitarsis*, *Celonites wahlenbergiae* and *Quartinia vagepunctata* should be put into context, nesting by the Masarinae (*sensu* Carpenter 1982) as a whole is outlined and discussed.

Basic nest types.— From a review of the published and present accounts of the nesting of the Masarinae it is possible to recognize seven basic nest types:

Nest type 1: a multicellular sub-vertical burrow in horizontal to sub-horizontal ground excavated by the nester, with an entrance turret constructed from earth extracted from within the burrow but with the excavated cells not containing constructed cells:

Four species of *Ceramius*: all species of Group 8 - *C. capicola* Brauns and *C. linearis* Klug (Gess and Gess 1980), *C. bicolor* (Thunberg) (Gess and Gess 1986) and *C. socius* Turner (Gess and Gess 1988b).

Nest type 2: a multicellular sub-horizontal burrow in vertical to sub-vertical ground excavated by the nester, with an entrance turret constructed from earth extracted from within the burrow, and with the walls of each excavated cell lined with cemented earth excavated within the burrow:

One species of *Masarina*: *M. familiaris* Richards (Gess and Gess 1988a).

Nest type 3: a multicellular sub-vertical burrow in horizontal to sub-horizontal ground excavated by the nester, with or without an entrance turret constructed from earth extracted from within the burrow, and with each excavated cell containing a constructed cell formed from earth excavated within the burrow:

Three species of Paragia: *P. (Paragia) tricolor* Smith (Houston 1984); *P. (Paragia) decipiens* Shuckard (Naumann and Cardale 1987); and *P. (Cygnea) vespiformis* Smith (Houston 1986).

Eleven species of *Ceramius*: Group 2a — *C. cerceriformis* Saussure (Gess and Gess 1988b); Group 2b — *C. clypeatus* Richards (Gess and Gess 1990); Group uncertain, probably 2b— *C. micheneri* (Gess and Gess 1990); all species of Group 3 —*C. nigripennis* Saussure (Gess and Gess 1986), *C. jacoti* Richards (Gess and Gess 1988b), *C. braunsi* Turner and *C. toriger* Schulthess (Gess and Gess 1990); the single species of Group 5— *C. lichtensteinii* (Klug) (Gess and Gess 1980); Group 6 —*C. rex* Saussure (Gess and Gess 1988b) and *C. metanotalis* Richards (Gess and Gess unpublished fieldnotes); Group 7—*C. tuberculifer* Saussure (Giraud 1871, Ferton 1901).

Two species of *Jugurtia*: *J. confusa* Richards (Gess and Gess 1980) and *J. braunsi* (Schulthess) (Gess and Gess unpublished field notes).

Nest type 4: a group of constructed earthen cells attached to plant stems or stones:

Six species of *Celonites*: *C. abbreviatus* (Villers) (Lichtenstein 1869 (as *C. apiformis* Fabricius), Ferton 1901, 1910, Bellmann 1984); *C. fischeri* Spinola (Bingham 1898 as reported in Richards 1962); *C. mayeti* Richards (Lichtenstein 1875, Ed. André 1884 as reported in Richards 1962); *C. jousseaumei* du Buysson (Richards 1962); and *C. andrei* Brauns (Brauns 1913); and in addition a putative nest of *C. promontorii* (Brauns) (Gess and Gess 1989).

Eight species of *Pseudomasaris*: *P. coquilletti* Rohwer (Richards 1963b); *P. edwardsii* (Cresson) (Torchio 1970); *P. maculifrons* (Fox) (Parker 1967); *P. occidentalis* (Cresson) (Hungerford 1937 as reported in Torchio 1970); *P. phaceliae* Rohwer (Parker 1967, Torchio 1970); *P. texanus* (Cresson) (Bequaert 1940 as reported in Torchio 1970); *P. vespoides* (Cresson) (Torchio 1970); and *P. zonalis* (Cresson) (Parker 1967).

One species of *Gayella*: *G. eumenoides* Spinola (Claude-Joseph 1930 as reported in Richards 1962).

Nest type 5: constructed earthen cells located in a pre-existing cavity; soil for cell construction collected from a quarry site at some distance from the nest:

One species of *Celonites*: *C. wahlenbergiae* (present paper).

Nest type 6: a self-excavated sloping burrow in friable soil with an excavated cell in which is an earthen cell constructed from soil collected from a quarry site at some distance from the nest:

One species of *Celonites*: *C. latitarsis* (present paper).

Nest type 7: a sub-vertical burrow in friable soil, surmounted by a sand and silk turret and having an excavated cell in which is a constructed sand and silk cell:

One species of *Quartinia*: *Q. vagepunctata* (present paper).

Ground nesting has been recorded for a further eleven species, however, the observations are too incomplete for these species to be attributed to the nest types as set out above: (*Paragia* (*Paragia*) *smithii* Saussure (Wilson 1869); *Rolandia maculata* (Meade-Waldo) and an undescribed species of *Riekia* (Houston 1984); *Ceramiopsis paraguayensis* Bertoni (almost certainly a synonym of *C. gestroi* Zavattari (Richards 1962)) (Bertoni 1922 as reported in Richards 1962); three species of *Ceramius*, Group 1 - *C. fonscolombei* Latreille (Fonscolombe 1835), Group 7 - *C. bischoffi* Richards (Richards 1963a), and Group 4 - *C. beyeri* Brauns (Brauns 1910, Gess and Gess 1988b); two species of *Trimeria*, *T. howardi* Bertoni (Zucchi et al. 1976 as reported in Houston 1984) and *T. buyssoni* Brethes (Neff and Simpson 1985); *Quartinia* sp. (Jacot Guillarmod personal communication), and *Quartinioides* sp. (Gess and Gess 1988a, 1989). Conflicting accounts have been given for *Masaris vespiformis* Fabricius. Morice (1900) suggested that this species is ground nesting and Ferton (1920) that it makes aerial mud cells.

Dorr and Neff (1982) described a nest in a beetle boring. The nest consisted of a linear series of four unlined cells separated by mud partitions. This they alleged to be a nest of *Pseudomasaris marginalis* (Cresson), however, confirmation is required.

Bonding agent.— Three bonding agents, water, nectar, and silk, are known to be used by masarines in nest construction.

Use of water in excavation and as the bonding agent is either stated or implied in all nesting accounts of Nest types 1, 2 and 3. In addition the inner surfaces of the cells of *Paragia* (*P.*) *tricolor* are polished and waterproofed with an unidentified substance (Houston 1984).

Nectar is the proven bonding agent employed by *Pseudomasaris edwardsii* of Nest type 4 (Torchio 1970). Circumstantial evidence, available to the present authors, furthermore suggests that nectar is used by *Celonites* of Nest types 4, 5 and 6.

The use of self-generated silk sets Nest type 7 as exemplified by *Q. vagepunctata* apart from all the others. The use of silk in nest building by wasps seems to be altogether uncommon. It has been noted for two eumenines, one ground nesting (Gess and Gess unpublished fieldnotes) and one nesting in pre-existing cavities (Weaving personal communication), and has been recorded for two social sphecids, one constructing aerial nests, *Microstigmus comes* Krombein (Myers 1934, Matthews and Starr 1984) and one nesting in pre-existing cavities, *Arpactophilus mimi* Naumann (Matthews and Naumann 1988). In both sphecid species the adult wasps secrete the silk from glands near the tip of the metasoma. Adult *Q. vagepunctata* observed appeared to produce silk from their mouths and it is suggested therefore that silk is most probably produced by the mandibular glands.

Using nectar or silk as a bonding agent frees the user from dependence on water, an often ephemeral resource in arid areas. The use of silk furthermore makes it possible for the users to construct nests in and with friable soil which otherwise becomes readily unstable under dry conditions.

Method of nest construction by ground nesters.— In the first three nest types water is carried from a water source in the crop. On arrival at the nest it is regurgitated and worked into the soil with the mandibles to form mud. The spoils of excavation are removed with the mandibles in the form of mud pellets which are either discarded, used for the construction of a turret or for the construction of cells.

In the sixth nest type exemplified by *C. latitarsis*, in which the burrow is excavated in friable soil, water is not used and the spoils of excavation are raked out and accumulate to form a tumulus. This is of particular note when the structure of the fore tarsi of *C. latitarsis* is compared with that of ten other Afrotropical species of *Celonites* (Gess 1992). Of those species compared, only *C. latitarsis* has widely expanded tarsomeres suitable for raking soil which suggests that its nest type may be unusual for *Celonites*.

Sand raking seems to be unusual not only for masarines but for Vespidae as a whole. Furthermore it seems that nesting in friable soil in the Vespidae is probably derived rather than primitive as in the Pompilidae and Sphecidae. Apart from *C. latitarsis* none of those species known to excavate nests in friable soil has fore tarsal sand rakes as possessed by many ground nesting Sphecidae and Pompilidae. Soil removal is effected by the mandibles as in those species excavating in non-friable soil. For example *Pseudepipona herrichii* (Saussure), a eumenine nesting in a vertical burrow in friable ground, removes sand particles with the mandibles one at a time (Spooner 1934 as in Spradbery 1973). The only recorded morphological modification for sand removal is that of the mouthparts of *Pterocheilus* (Bohart 1940) for which nesting in vertical burrows in friable soil by two species has been recorded (Isely 1914, Evans 1956). Amongst the masarines turretless inclined burrows excavated in sandy ground have been recorded for an undescribed species of *Riekia* and for *Rolandia maculata* (Houston 1984). Unfortunately the method of excavation was not noted and the nests were incomplete.

Not only is the substrate and the method of excavation of the burrows of Nest type 6 very different in nature from that of Nest type 3 but, as importantly, so is the nature of and method of construction of the cells. Whereas the earthen cells of Nest type 3 are constructed from soil quarried within the burrow and bonded with water those of Nest type 6 are constructed from soil quarried at some distance from the burrow and bonded not with water but most probably with nectar. The method of construction and nature of the earthen cells of Nest type 6 as exemplified by *C. latitarsis* in no way differs from that of Nest type 5 as exemplified by *C. wahlenbergiae* nesting in pre-existing burrows and that of Nest type 4 as exemplified by the aerial nesting *Celonites* species.

Evolutionary sequence.— A possible sequence is discernable within the Masarinae from excavated burrows with excavated cells only (Nest type 1) through excavated burrows with constructed earthen cells within excavated cells with earth for construction being derived from within the burrow (Nest type 3) to the presumably more advanced construction of aerial earthen cells (Nest type 4) (discussed in Gess and Gess 1980).

A further possible sequence within the genus *Celonites* is here suggested, that is a return to the ground from aerial earthen cells (Nest type 4) through constructed earthen cells in pre-existing cavities in the ground (Nest type 5) to self excavated burrows with constructed earthen cells within excavated cells with earth for construction being mined outside the burrow (Nest type 6).

This second sequence is suggested by the method of construction of Nest type 6, notably the sand raking behaviour with the consequent possession of sand-rakes as yet not recorded for any other masarines, soil for cell construction being obtained from a site at some distance from the nest not from within the nest, and the bonding agent being nectar as used in Nest type 4 and 5 not water as is used in Nest type 3.

Nest type 7 is distinct and is possibly derived from a vertical burrow excavated in stable friable soil without the use of a bonding agent.

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